



Processes regulating the initiation and postejaculatory resumption of copulatory behavior in male hamsters



Owen R. Floody*

Department of Psychology and Program in Neuroscience, Bucknell University, Lewisburg, PA 17837, United States

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ABSTRACT

Studies using factor analysis have helped describe the organization of copulatory behavior in male rodents. However, the focus of these studies on a few traditional measures may have limited their results. To test this possibility, 74 sexually-experienced male hamsters were observed as they copulated with stimulus females. The measures collected exceeded the conventional ones in number, variety and independence. The factor analysis of these data revealed a structure with seven factors collectively accounting for 80% of the variance. Most resembled the factors in previous reports, reinforcing the contributions that the processes suggested by these factors make to the organization of male behavior. But several other factors were more novel, possibly reflecting the use of measures that were novel or revised for greater independence. The most interesting of these were two factors focusing on early steps in the progression leading to ejaculation. Importantly, both incorporated measures from each of the three copulatory series that were observed. Past work suggests that independent processes control the times required to initiate copulation and later resume it after an ejaculation. In contrast, these results suggest the existence of two processes, each of which contributes to both the initiation and reinitiation of copulation.

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1. Introduction

Copulation in male rodents has long attracted scientific attention for reasons including its biological importance, responsiveness to hormonal and other manipulations, and incorporation of distinctive elements that lend themselves to behavioral analysis. The organization of copulatory behavior can and has been studied in a variety of ways. The most common approach begins by distinguishing mounts, intromissions and ejaculations. It then focuses on a standard set of eight dependent variables describing the timing and frequency of these basic elements (e.g., Sachs, 1978). This includes two measures that are specific to events occurring early in mating, i.e., the mount and intromission latencies (the delays preceding the first mount and intromission, respectively). The remaining measures refer to events or intervals tied to specific ejaculations, and thus to specific copulatory series, each including an ejaculation and the behaviors that immediately precede it. The standard measures of this type include ejaculation latency (the interval separating a series' first intromission from its concluding ejaculation), postejaculatory interval (the delay between an ejaculation and the next intromission), mount frequency (the number of mounts in a series),

intromission frequency (the number of intromissions in a series), interintromission interval (the average time separating successive intromissions in a series), and intromission ratio (the proportion of all mounts and intromissions in a series that were intromissions). Except for intromission ratio, all of these are thought to relate inversely to the overall efficiency, or quality, of copulatory performance (the amount of time and effort required to achieve ejaculation).

Average levels of these measures can be, and usually are, compared across experimental conditions. Alternatively, a powerful but less common approach to their analysis relies on the statistical method of factor analysis. This uses intercorrelations of measures to define the minimal set of conceptual variables or "factors" required to explain most of the interindividual variability in performance. Though determined by all measures, each factor typically is identified with a subset of variables that relate closely to it and each other. These relations are expressed in factor "loadings," and it typically is the few measures that load most heavily on a factor that determine how that factor is labeled and interpreted.

Early factor analytic studies of sexual behavior focused on the performance of male rats in the first copulatory series (Dewsbury, 1979; Pfaus et al., 1990; Sachs, 1978). These converged impressively on similar factor structures. First, each included a Copulatory Rate factor identified with ejaculation latency, interintromission interval and postejaculatory interval. Second, each included an Initiation

* Tel.: +1 570 577 1200; fax: +1 570 577 7007.
 E-mail address: ofloody@bucknell.edu

factor identified with the mount and intromission latencies. Third, most described an Efficiency factor identified with mount frequency and intromission ratio. Even the remaining studies reported an Efficiency factor, but one defined mainly by the frequencies of mounts and intromissions. Possibly as a consequence of this variability in definition, some analyses described only the aforementioned three factors (Dewsbury, 1979) whereas others found intromission frequency to define a fourth factor (Pfaus et al., 1990; Sachs, 1978).

Other species in which male behavior has been subjected to factor analysis include deer mice (Dewsbury, 1979) and hamsters (Floody, 2011). Despite some subtle differences, their factor structures resemble those reported for rats in their incorporation of (a) an Initiation factor defined mainly by the mount and intromission latencies, (b) an Efficiency factor identified primarily with the combination of mount frequency and intromission ratio, and, (c) an intromission-focused factor identified largely with intromission frequency. On the other hand, the species differ strongly on the existence of a Copulatory Rate factor. This joint product of ejaculation latency, interintromission interval and postejaculatory interval is the most consistent result of factor analyses of rat copulatory performance, but appears to be absent altogether from the factor structures of deer mice and hamsters.

Though these analyses have advanced our understanding of how male behavior is organized, they raise several possible concerns. One of the strengths of factor analysis is its ability to test interrelations among many potential measures, often guiding a subsequent selection of those that best define the operative conceptual variables. This capacity has not been seriously tested by analyses limited to just 14 variables. Though this limitation might not merit attention if the selected variables already were known to be optimal, the conventional measures of male behavior seem limited in several ways. First, they clearly are incomplete. Male reproductive behavior involves much more than just mounts, intromissions and ejaculations. This has been recognized all along (e.g., Sachs, 1978; Pfaus et al., 1990), but broader measures have received little attention, probably because of the premium placed on direct comparisons of results across studies. Second, some standard measures enter into the calculation of others. For example, interintromission interval is jointly determined by ejaculation latency and intromission frequency. Similarly, intromission ratio is determined by both mount and intromission frequencies. These definitions introduce interdependencies that could influence how these variables behave in factor analysis. Third, latencies have been defined inconsistently both within and across studies. On the one hand, ejaculation latency always is defined in relation to the first intromission in the same copulatory series. In contrast, mount and intromission latencies have been defined with respect to the introduction of the stimulus female (Dewsbury, 1979; Pfaus et al., 1990) or the initial social contact (Floody, 2011). Fourth, because of this, latencies sometimes have been defined so as to essentially guarantee high correlations and, eventually, high loadings on a common factor. In particular, tying mount and intromission latencies to a common reference point guarantees that the second will always exceed the first: The reverse is impossible because each intromission is considered to incorporate a mount, so that the two latencies become equal if no separate mount is observed. In fact, this situation is a common one, resulting in an even closer correlation between the two latencies than the definitions require.

Of these issues, the second seems the least problematic. The fact that interintromission interval depends on both ejaculation latency and intromission frequency ensures that it will not be fully determined by either one of the others. Consistent with this interpretation, few prior studies have described factors heavily loaded by all three of these measures (Dewsbury, 1979; Floody, 2011; Pfaus et al., 1990; Sachs, 1978). The potential for undue influence seems

greater for intromission ratio, which does generally cluster with one of its determinants, mount frequency, probably due to a difference in variability between the two contributing frequencies (Dewsbury, 1979; Floody, 2011; Pfaus et al., 1990; Sachs, 1978). However, any clustering of intromission ratio and mount frequency seems then to be a product of the behavior, and one that captures relationships across measures in the intended way.

The remaining issues all seem to merit attention. But it would be difficult to address all at once. Accordingly, the present project was designed to address these issues to just a limited extent. It begins with a larger range of measures, but few are completely novel. Issues relating to the definition of latency measures are addressed partly by emphasizing the sequential nature of the behavior and defining each latency with reference to the immediately preceding step in the normal sequence, exactly as is routinely done in the case of ejaculation latency. This increases the consistency of latency definitions within this study and also should eliminate any spurious interrelationships among them. Collectively, these changes should provide a new perspective on the organization of male behavior. This has the potential to reveal new organizational features at the same time that it tests the effectiveness of previously established principles.

2. Method

These data were collected in the course of a larger study examining the impact on the organization of male behavior of stimulus females that moved in species-typical or -atypical ways between intromissions (Floody, unpublished). Specifically, that study included three conditions that were presented in counterbalanced orders and differed in whether and how the stimulus female was moved. However, all of the data to be presented here were collected from each male's one control test, during which the mating pair was completely undisturbed. In the context of the larger study, these tests were designed to establish normative patterns of behavior.

2.1. Animals and housing

Complete data were collected from 74 male golden hamsters (LVG:Lak outbred strain) that averaged 29 weeks of age (95% CI = 3) at the start of testing and were purchased from Charles River Laboratories (Wilmington, MA) or bred from Charles River stock. High levels of sexual experience were ensured by a screening process requiring ejaculation within 10 min in at least five of seven tests at 4-day intervals. In fact, because of a delay in the start of data collection, most males repeated this series of screening tests and so entered experimental testing having ejaculated in 10 earlier encounters.

The stimuli included 18 adult female hamsters. These were selected to be comparable to or slightly smaller than the males, though the extent of the size difference varied across tests. Each female was bilaterally ovariectomized at least 2 weeks before use and brought into hormone-induced estrus by treatment with 10 μ g of estradiol benzoate in 0.05 ml of peanut oil injected subcutaneously about 48 h before testing, followed by a similar injection of 500 μ g of progesterone at approximately 6 h before use. The facilitation of lordosis by this treatment was confirmed immediately before each use of a female by observing her interact briefly with a stimulus male. Each female then served in as many as five tests spanning approximately 15 min and including up to six ejaculations (those in some of the tests excluded from this report were divided between two females). Lordosis responses in estrous female hamsters routinely persist for at least this long and through at least this number of ejaculations (Floody, 2013; Floody and Lisk, 1989).

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